

ON IMPULSIVE REACTION-DIFFUSION MODELS IN HIGHER DIMENSIONS

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ABSTRACT. Assume that $N_m(x)$ denotes the density of the population at a point x at the beginning of the reproductive season in the m th year. We study the following impulsive reaction-diffusion model for any $m \in \mathbb{Z}^+$

$$\begin{cases} u_t^{(m)} = \operatorname{div}(A \nabla u^{(m)} - a u^{(m)}) + f(u^{(m)}) & \text{for } (x, t) \in \Omega \times (0, 1] \\ u^{(m)}(x, 0) = g(N_m(x)) & \text{for } x \in \Omega \\ N_{m+1}(x) := u^{(m)}(x, 1) & \text{for } x \in \Omega \end{cases}$$

for some functions f, g , a drift a and a diffusion matrix A and $\Omega \subset \mathbb{R}^n$. Study of this model requires a simultaneous analysis of the differential equation and the recurrence relation. When boundary conditions are hostile we provide critical domain results showing how extinction versus persistence of species arises, depending on the size and geometry of the domain. We show that there exists an *extreme volume size* such that for $|\Omega|$ falls below this size the species is driven extinct, regardless of the geometry of the domain. To construct such extreme volume sizes and critical domain sizes, we apply Schwarz symmetrization rearrangement arguments, the classical Rayleigh-Faber-Krahn inequality and the spectrum of uniformly elliptic operators. The critical domain results provide qualitative insight regarding long-term dynamics for the model. In addition, we provide an explicit formula for the spreading speed of propagation for this model. The remarkable point is that the roots of the spreading speed formula, as a function of drift, are exactly the values that blow up the critical domain dimensions, just like the classical Fisher's equation with advection. At the end, we provide applications of our main results to certain biological reaction-diffusion models regarding marine reserve, terrestrial reserve, insect pest outbreak and population subject to climate change.

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1. INTRODUCTION

Impulsive reaction-diffusion equation models for species with distinct reproductive and dispersal stages were proposed by M. Lewis and B. Li in [26]. These models can be considered as a description for a seasonal birth pulse plus nonlinear mortality and dispersal throughout the year. Alternatively, they can describe seasonal harvesting, plus nonlinear birth and mortality as well as dispersal throughout the year. The population of a species at the beginning of year m is denoted by $N_m(x)$. We assume that reproduction (or harvesting) occurs at the beginning of the year, via a discrete time map, g , after which there is birth, mortality and dispersal via a reaction-diffusion equivalently for a population with density $u^{(m)}(x, t)$. At the end of this year the density $u^{(m)}(x, 1)$ provides the population density for the start of year $m + 1$, $N_{m+1}(x)$. We examine solutions of the following system for any $m \in \mathbb{Z}^+$

$$(1.1) \quad \begin{cases} u_t^{(m)} = \operatorname{div}(A \nabla u^{(m)} - a u^{(m)}) + f(u^{(m)}) & \text{for } (x, t) \in \Omega \times (0, 1], \\ u^{(m)}(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u^{(m)}(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where Ω is a set in \mathbb{R}^n , A is a constant symmetric positive definite matrix and a is a constant vector. Suppose also that $f(\cdot)$ is the Kolmogoroff, Petrowsky, and Piscounoff (KPP) type nonlinearity and $g(\cdot)$ is a positive nondecreasing function in \mathbb{R}^+ .

The above equation (1.1) defines a recurrence relation for $N_m(x)$ as

$$(1.2) \quad N_{m+1}(x) = Q[N_m(x)] \quad \text{for } x \in \Omega \subset \mathbb{R}^n,$$

where $m \geq 0$ and Q is an operator that depends on A, a, f, g . Most of the results provided in this paper are valid in any dimensions however we shall focus on the case of $n \leq 3$ for applications. For notational convenience we drop superscript (m) for $u^{(m)}(x, t)$, rewriting it as $u(x, t)$. The remarkable point about the impulsive reaction-diffusion equation (1.1)-(1.2) is that it is a mixture of a differential equation and a recurrence relation. Therefore, one may expect that the analysis of this model requires a simultaneous analysis of the KPP and discrete type.

The discrete time models of the form (1.2) are studied extensively in the literature, in particular in the foundational work of Weinberger [43], where $N_m(x)$ represents the gene fraction or population density at time n at the point x of the habitat and Q is an operator on a certain set of functions on the habitat. It is shown by Weinberger [43] that under a few biologically reasonable hypothesis on the operator Q the results similar to those for the Fisher and KPP types for models (1.2) hold. In other words, given a direction vector e , the recurrence relation (1.2) admits a nonincreasing planar traveling wave solution for every $c \geq c^*(e)$ and, more importantly, there will be a spreading speed $c^*(e)$ in the sense that, a new mutant or population which is initially confined to a bounded set spreads asymptotically at speed $c^*(e)$ in direction e . This falls under the general Weinberger type given in equation (1.2).

In this paper, we provide critical domain size for extinction versus persistence of populations for impulsive reaction-diffusion models of the form (1.1) defined on domain $\Omega \subset \mathbb{R}^n$. It is known that the geometry of the domain has fundamental impacts on qualitative behaviour of solutions of equations in higher dimensions. We consider domains with various geometric structures in dimensions $n \geq 1$ including convex and concave domains and also domains with smooth and non smooth boundaries.

Note that for the standard Fisher's equation with the drift in one dimension that is

$$(1.3) \quad u_t = du_{xx} - au_x + f(u) \quad \text{for } (x, t) \in \Omega \times \mathbb{R}^+,$$

the critical domain size for the persistence versus extinction is

$$(1.4) \quad L^* := \frac{2\pi d}{\sqrt{4df'(0) - a^2}},$$

when $\Omega = (0, L)$ and the speeds of propagation to the right and left are

$$(1.5) \quad c_{\pm}^* = 2\sqrt{df'(0)} \pm a,$$

when $\Omega = \mathbb{R}$. For more information regarding the minimal domain size, we refer interested readers to Speirs and Gurney [40], Lewis et al. [25] and Pachepsky et al. [35] and references therein. The interesting point is that $c_{\pm}^*(a)$ is a linear function of a and L^* as a function of a blows up to infinity exactly at roots of $c_{\pm}^*(a)$.

Notation 1.1. Throughout this paper the matrix $I = (\delta_{i,j})_{i,j=1}^n$ stands for the identity matrix, the matrix A is defined as $A = (a_{i,j})_{i,j=1}^n$ and the vector a is $a = (a_i)_n$. The matrix A and the vector a have constant components unless otherwise is stated. Throughout this paper $j_{m,1}$ is the first positive zero of the Bessel function J_m for any $m \geq 0$ and Γ stands for the Gamma function.

We assume that g is a continuous positive function in \mathbb{R}^+ and $g(0) = 0, g'(0) > 0$ and there exists a positive constant $M \in (0, \infty]$ such that for $g(N)$ is nondecreasing for $0 < N \leq M$. This implies that the function g does not have to be monotone on the entire positive real line. In other words, monotonicity of g is required only on a subset of \mathbb{R}^+ . We also assume that the quotient $\frac{g(N)}{N}$ is nonincreasing in \mathbb{R}^+ . Note that the linear function

$$(1.6) \quad g(N) = cN,$$

where c is a positive constant satisfies all of the above assumptions. For the above g , model (1.1) recovers the classical Fisher's equation introduced by Fisher in [16] and Kolmogorov, Petrowsky, and Piscounoff in [23] in 1937.

One can consider nonlinear functions for g like the Ricker function that is

$$(1.7) \quad g(N) = Ne^{r(1-N)},$$

where r is a positive constant. For the optimal stocking rates for fisheries mathematical biologists often apply the Ricker model [38] introduced in 1954 to study the salmon population in the Pacific northwest, where they spawn in river beds and can spawn on top of a previous site. The Ricker function is nondecreasing for $0 < N \leq M = \frac{1}{r}$ and satisfies all of the assumptions. Note also that the Beverton-Holt function

$$(1.8) \quad g(N) = \frac{(1 + \lambda)N}{1 + \lambda N},$$

where $\lambda > 0$ is a nondecreasing. The Beverton-Holt model was introduced in the context of fisheries by Beverton and Holt [6] in 1957. Another example is the Skellam function

$$(1.9) \quad g(N) = R(1 - e^{-bN}),$$

where R and b are positive constants. This function was introduced by Skellam in 1951 in [39] to study population density for animals such as birds which have contest competition for nesting sites. Note that the Skellam function behaves similar to the Beverton-Holt function and it is nondecreasing for any $N > 0$. We shall use these functions in the application section (Section 4). We now fix the following growth conditions on the function g .

Definition 1.1. We say that a function $g(N)$ is

- (i) *sublinear* if there exists a positive constant $\bar{M} \leq M$ such that $g(N) \leq g'(0)N$ for $0 < N < \bar{M}$.
- (ii) *upper sublinear* if it is sublinear and there exist a differentiable function h for $h(0) = h'(0) = 0$ and a constant $\tilde{M} \leq M$ so that $g(N) \geq g'(0)N - h(N)$ for $0 < N < \tilde{M}$.

Suppose that $a = 0$ and $A = 0$ then $u(x, t)$ only depends on time and not space meaning that individuals do not advect or diffuse. Assume that N_m represents the number of individuals at the beginning of reproductive stage in the m th year. Then

$$(1.10) \quad \begin{cases} u_t(t) = f(u(t)) & \text{for } t \in (0, 1], \\ u(0) = g(N_m), \\ N_{m+1} := u(1). \end{cases}$$

Straightforward calculations show that

$$(1.11) \quad \int_{g(N_m)}^{N_{m+1}} \frac{d\omega}{f(\omega)} = 1.$$

Note that a positive constant equilibrium of this relation satisfies

$$(1.12) \quad \int_{g(N)}^N \frac{d\omega}{f(\omega)} = 1.$$

Assume that f is sublinear and $f(0) = g(0) = 0$ then

$$(1.13) \quad 1 = \int_{g(N)}^N \frac{d\omega}{f(\omega)} \geq \frac{1}{f'(0)} \int_{g(N)}^N \frac{d\omega}{\omega} = \frac{1}{f'(0)} \ln \left| \frac{N}{g(N)} \right|.$$

From the fact that the equation (1.10) has always has the trivial equilibria zero and from properties of the function g we get

$$(1.14) \quad e^{f'(0)} g'(0) > 1.$$

Throughout this article we assume that there exists a positive equilibrium N^* for (1.12) such that (1.14) holds.

The organization of the paper is as follows. We investigate how the geometry and size of the domain Ω affects persistence vs extinction of the species. We consider various types of domain, including a n -hyperrectangle, a ball of radius R , and a general domain with smooth boundary, to construct critical domain sizes and extreme volume size (Section 2). We provide an explicit formula for the spreading speed of propagation for the impulsive reaction-diffusion model (1.1) in any direction (Section 3). We then provide applications of the main results to models for marine reserve, terrestrial reserve, insect pest outbreaks and populations subject to climate change (Section 4). At the end, we provide proofs for our main results and discussions.

2. GEOMETRY OF THE DOMAIN FOR PERSISTENCE VS EXTINCTION

A habitat boundary not only can be considered as a natural consequence of physical features such as rivers, roads, or (for aquatic systems) shorelines but also it can come from interfaces between different types of ecological habitats such as forests and grasslands. Boundaries can induce various effects in population dynamics. They can affect movement patterns, act as a source of mortality or resource subsidy, or can function as a unique environment with its own set of rules for population interactions. See Fagan et al. [13] for further discussion. Note that a boundary can have different effects on different species. For example, a road may act as a barrier for some species but as a source of mortality for others. Since a boundary can have different effects on different species, the presence of a boundary can influence community structure in ways that are not completely obvious from the ways in which they affect each species, see Cantrell and Cosner [9, 10] for more information.

In this section, we consider the following impulsive reaction-diffusion model on domains with hostile boundaries to explore persistence versus extinction

$$(2.1) \quad \begin{cases} u_t = \operatorname{div}(A \nabla u - au) + f(u) & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where Ω is a bounded domain in \mathbb{R}^n , a is a vector in \mathbb{R}^n and A is a constant positive definite symmetric matrix.

In what follows we provide critical domain sizes for various domains depending on the geometry of the domain. We shall postpone the proofs of these theorems to the end of this section. We start with the critical domain size for a n -hyperrectangle (n -orthotope).

Theorem 2.1. *Assume that $\Omega = [0, L_1] \times \cdots \times [0, L_n]$ where L_1, \dots, L_n are positive constants, $A = d(\delta_{i,j})_{i,j=1}^n$ and the advection a is a vector field in \mathbb{R}^n . Suppose also that f, g are upper sublinear functions satisfying (1.14). Then, critical domain dimensions L_1^*, \dots, L_n^* satisfy*

$$(2.2) \quad \sum_{i=1}^n \frac{1}{[L_i^*]^2} = \frac{1}{d\pi^2} \left[\ln(e^{f'(0)} g'(0)) - \frac{|a|^2}{4d} \right],$$

where $\ln(e^{f'(0)} g'(0)) > \frac{|a|^2}{4d}$. More precisely, when

$$(2.3) \quad \sum_{i=1}^n \frac{1}{[L_i]^2} > \frac{1}{d\pi^2} \left[\ln(e^{f'(0)} g'(0)) - \frac{|a|^2}{4d} \right],$$

and g grows linearly then $N_m(x)$ decays to zero that is $\lim_{m \rightarrow \infty} N_m(x) = 0$ and when

$$(2.4) \quad \sum_{i=1}^n \frac{1}{[L_i]^2} < \frac{1}{d\pi^2} \left[\ln(e^{f'(0)} g'(0)) - \frac{|a|^2}{4d} \right],$$

and g grows superlinearly then $\liminf_{m \rightarrow \infty} N_m(x) \geq \bar{N}(x)$ where $\bar{N}(x)$ is a positive equilibrium. In addition, critical domain dimensions can be arbitrarily large when $\ln(e^{f'(0)} g'(0)) < \frac{|a|^2}{4d}$.

Suppose that the domain Ω is a n -hypercube. Then the critical domain size is explicitly given by the following corollary.

Corollary 2.1. *Suppose that assumptions of theorem 2.1 hold. In addition, let $L_1 = \dots = L_n = L > 0$. Then the critical domain dimension is*

$$(2.5) \quad L^* := \begin{cases} 2\pi d \sqrt{\frac{n}{4d[f'(0) + \ln(g'(0))] - |a|^2}}, & \text{if } 4d[f'(0) + \ln(g'(0))] - |a|^2 > 0, \\ \infty, & \text{if } 4d[f'(0) + \ln(g'(0))] - |a|^2 < 0. \end{cases}$$

We now put the above results in a figure to clarify the relationship between the critical domain dimension and the advection in two dimensions, $n = 2$.

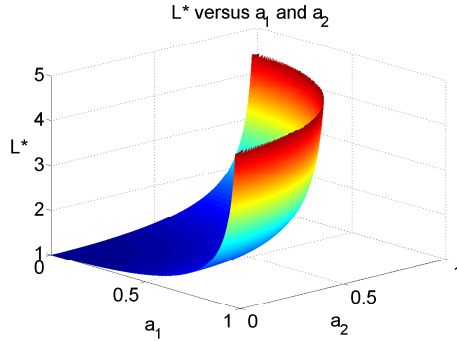


FIGURE 1. Critical domain dimension L^* as a function of $a = (a_1, a_2)$.

Note that for the case $n = 1$ and $a = 0$, the minimal domain size L^* was given by Lewis-Li in [26]. In addition, one can compare the critical domain dimension (2.5) for the impulsive reaction-diffusion model (1.1) in higher dimensions to the one given by (1.4) for the classical Fisher's equation in one dimension. We now provide a similar result for a critical domain dimension when the domain is a ball of radius R .

Theorem 2.2. *Suppose that $\Omega = B_R$ where B_R is the ball of radius R and centred at zero, $A = d(\delta_{i,j})_{i,j=1}^m$ and the drift a is a divergence free vector field. Suppose also that f, g are upper sublinear functions satisfying (1.14). Then the critical domain dimension is*

$$(2.6) \quad R^* := j_{n/2-1,1} \sqrt{\frac{d}{\ln(g'(0)) + f'(0)}},$$

in the sense that if $R < R^*$ and g grows linearly then $\lim_{m \rightarrow \infty} N_m(x) = 0$ and if $R > R^*$ and if g grows superlinearly then $\liminf_{m \rightarrow \infty} N_m(x) \geq \bar{N}(x)$ where $\bar{N}(x)$ is a positive equilibrium.

Theorem 2.2 is a generalized version of the standard island case (two-dimensional space) for discussing the persistence and extinction of a species.

From now on we consider a more general domain $\Omega \subset \mathbb{R}^n$ with a smooth boundary. Our main goal is to provide sufficient conditions on the volume and on the geometry of the domain Ω for the extinction of populations. To be able to work with general domains we borrow Schwarz symmetrization rearrangement arguments from mathematical analysis. In what follows shortly, we introduce this symmetrization argument and then we apply it to eigenvalue problems associated to (1.1). We refer interested readers to the lecture

notes of Burchard [8] and references therein for more information. Let Ω be a measurable set of finite volume in \mathbb{R}^n . Its symmetric rearrangement Ω^* is the following ball centred at zero whose volume agrees with Ω ,

$$(2.7) \quad \Omega^* := \{x \in \mathbb{R}^n; \alpha_n |x|^n < |\Omega|\}.$$

For any function $\phi \in L^1(\Omega)$, define the distribution function of ϕ as

$$(2.8) \quad \mu_\phi(t) := |\{x \in \Omega; \phi(x) > t\}|,$$

for all $t \in \mathbb{R}$. The function μ_ϕ is right-continuous and non increasing and as $t \rightarrow \infty$ we have $\mu_\phi \rightarrow 0$. Similarly, as $t \rightarrow -\infty$ we have $\mu_\phi \rightarrow |\Omega|$. Now for any $x \in \Omega^* \setminus \{0\}$ define

$$(2.9) \quad \phi^*(x) := \sup\{t \in \mathbb{R}, \mu_\phi(t) \geq \alpha_n |x|^n\}.$$

The function ϕ^* is clearly radially symmetric and non increasing in the variable $|x|$. By construction, ϕ^* is equimeasurable with ϕ . In other words, corresponding level sets of the two functions have the same volume,

$$(2.10) \quad \mu_\phi(t) = \mu_{\phi^*}(t),$$

for all $t \in \mathbb{R}$. An essential property of the Schwarz symmetrization is the following: if $\phi \in H_0^1(\Omega)$, then $|\phi|^* \in H_0^1(\Omega^*)$ and

$$(2.11) \quad |||\phi|^*||_{L^2(\Omega^*)} = ||\phi||_{L^2(\Omega)},$$

and

$$(2.12) \quad |||\nabla|\phi|^*||_{L^2(\Omega^*)} = ||\nabla\phi||_{L^2(\Omega)}.$$

One of the main applications of this rearrangement technique is the resolution of optimization problems for the eigenvalues of some second-order elliptic operators on Ω . Let $\lambda_1(\Omega)$ denote the first eigenvalue of the Laplace operator $-\Delta$ with Dirichlet boundary conditions in an open bounded smooth set $\Omega \subset \mathbb{R}^n$ that is given by the Rayleigh-Ritz formula

$$(2.13) \quad \lambda_1(\Omega) = \inf_{||\phi||_{L^2(\Omega)}=1} ||\nabla\phi||_{L^2(\Omega)}^2.$$

It is well-known that $\lambda_1(\Omega) \geq \lambda_1(\Omega^*)$ and that the inequality is strict unless Ω is a ball. Since $\lambda_1(\Omega^*)$ can be explicitly computed, this result provides the classical Rayleigh-Faber-Krahn inequality, which states that

$$(2.14) \quad \lambda_1(\Omega) \geq \lambda_1(\Omega^*) = \left(\frac{|B_1|}{|\Omega|}\right)^{2/n} j_{n/2-1,1}^2,$$

where $j_{m,1}$ is the first positive zero of the Bessel function J_m . More recently, Hamel, Nadirishvili and Russ in [?] provided an extension of the above result to the operator

$$(2.15) \quad -\operatorname{div}(A\nabla) + a \cdot \nabla + V,$$

with Dirichlet boundary conditions where the symmetric matrix field A is in $W^{1,1}(\Omega)$, the vector field (drift) $a : L^1(\Omega) \rightarrow \mathbb{R}^n$ and potential V that is a continuous function in $\bar{\Omega}$. Throughout this paper, we call a matrix A *uniformly elliptic* on $\bar{\Omega}$ whenever there exists a positive constant d such that for all $x \in \bar{\Omega}$ and for all $\zeta \in \mathbb{R}^n$,

$$(2.16) \quad A(x)\zeta \cdot \zeta \geq d|\zeta|^2.$$

Consider the following eigenvalue problem,

$$(2.17) \quad \begin{cases} -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi &= \lambda(A, a, \Omega)\phi & \text{in } \Omega, \\ u &= 0 & \text{on } \partial\Omega, \end{cases}$$

it is shown in [19] that when $\Omega \in C^{2,\alpha}$ for some $0 < \alpha < 1$, the matrix A is uniformly elliptic and $a : L^\infty(\Omega) \rightarrow \mathbb{R}^n$ where $||a||_\infty \leq \tau$ for $\tau \geq 0$, then the first eigenvalue of (2.17) admits the following lower bound;

$$(2.18) \quad \lambda_1(A, a, \Omega) \geq \lambda_1(d(\delta_{i,j}), \tau e_r, \Omega^*).$$

Here $\Omega^* = B_R$ is the ball of radius

$$(2.19) \quad R = \left(\frac{|\Omega|}{\alpha_n}\right)^{1/n},$$

for $\alpha_n := |B_1| = \frac{\pi^{\frac{n}{2}}}{\Gamma(1+\frac{n}{2})}$. In addition, equality in (2.18) holds only when, up to translation, $\Omega = \Omega^*$ and $a = \tau e_r$ for $e_r = \frac{x}{|x|}$.

We are now ready to develop sufficient conditions for the extinction of population on various geometric domains. The remarkable point here is that the volume of the domain Ω is the key point for the extinction rather than the other aspects of the domain. The following theorems imply that for some general domain Ω there is an extreme volume size, V_{ex} , such that when $|\Omega| < V_{ex}$ extinction must occur for the population living in the habitat. The following theorem provides an explicit formula for such an extreme volume size for any open bounded domain with a smooth boundary.

Theorem 2.3. *Let A be uniformly elliptic, f, g be sublinear functions satisfying (1.14) and the vector field a be divergence free. Suppose that $\Omega \subset \mathbb{R}^n$ is an open bounded domain with smooth boundary and $|\Omega| < V_{ex}$ where*

$$(2.20) \quad V_{ex} := \frac{1}{\Gamma(1 + \frac{n}{2})} \left(\frac{d\pi j_{\frac{n}{2}-1,1}^2}{f'(0) + \ln(g'(0))} \right)^{\frac{n}{2}},$$

and $j_{k,1}$ stands for the first positive root of the Bessel function J_k . Then $\lim_{m \rightarrow \infty} N_m(x) = 0$ for any $x \in \Omega$.

Theorem 2.3 states that the addition of incompressible flow to the impulse reaction-diffusion problem can only make the critical domain size larger but never smaller.

Corollary 2.2. *In two dimensions, it is known that $j_{\frac{n}{2}-1,1} = j_{0,1} \approx 2.408$. Therefore the extreme volume size is*

$$(2.21) \quad V_{ex} = \frac{d\pi j_{0,1}^2}{f'(0) + \ln(g'(0))}.$$

Corollary 2.3. *In three dimensions, $j_{\frac{n}{2}-1,1} = j_{1/2,1} = \pi$ and $\Gamma(1 + \frac{n}{2}) = \Gamma(\frac{5}{2}) = \frac{3\sqrt{\pi}}{4}$. Therefore,*

$$(2.22) \quad V_{ex} = \frac{4\pi^4 d}{3} \sqrt{\frac{d}{[f'(0) + \ln(g'(0))]^3}}.$$

The fact that a hyperrectangle (or n -orthotope) does not have a smooth boundary implies that Theorem 2.3 is not applied to these types of geometric shapes. In what follows, we provide an extreme volume size result for a hyperrectangle in the light of Theorem 2.1.

Theorem 2.4. *Suppose that $\Omega = [0, L_1] \times \cdots \times [0, L_n]$ and $A = d(\delta_{i,j})_{i,j=1}^n$ where L_1, \dots, L_n and d are positive constants and a is a constant vector field. Assume that f, g are sublinear functions satisfying (1.14). If $|\Omega| \leq V_{ex}$ for*

$$(2.23) \quad V_{ex} := \begin{cases} \left(\frac{4d^2\pi^2 n}{4d[f'(0) + \ln(g'(0))] - |a|^2} \right)^{n/2} & \text{if } 4d[f'(0) + \ln(g'(0))] > |a|^2, \\ \infty, & \text{if } 4d[f'(0) + \ln(g'(0))] < |a|^2. \end{cases}$$

Then $\lim_{m \rightarrow \infty} N_m(x) = 0$ for any $x \in \Omega$.

We shall end this section by briefly explaining the divergence free concept that appeared in Theorem 2.2 and Theorem 2.3. The assumption $\operatorname{div} a = 0$ implies that the flow field is incompressible. This would be the case, for example, for water, but not for air. It also means that the following integral vanishes

$$(2.24) \quad \int_{\partial\Gamma} a \cdot n \, dS = 0,$$

by the divergence theorem. Here Γ is a smooth subset of the domain Ω (possibly non-proper), and n is the outwardly oriented unit normal vector. The integral quantity which is interpreted as the total flow out of Γ . This implies that the addition of incompressible flow to the problem cannot make the critical volume size any smaller, although it could make it larger. Indeed, even in the simple case of one dimension an incompressible flow term of the form $a \equiv C$, where C is a constant, can drive the critical domain size to infinity.

3. SPREADING SPEED

In this section, we provide an explicit formula of spreading speed propagation for (1.1)-(1.2) in $e = (e_1, \dots, e_n) \in \mathbb{R}^n$ direction. In addition, we compute the direction e such that the roots of the spreading speed as a function of advection coincide with the values for which critical domain dimensions, given as Theorem 2.1 and Corollary 2.1, tend to infinity. As we mentioned earlier, for the standard Fisher's equation in one dimension the critical domain size and the speed of propagation are given by

$$(3.1) \quad L^* := \frac{2\pi d}{\sqrt{4df'(0) - a^2}},$$

and

$$(3.2) \quad c_{\pm}^* = 2\sqrt{df'(0)} \pm a,$$

respectively. And roots of the spreading speed c_{\pm}^* as a function of a are exactly the values that for which L^* approaches infinity.

Throughout this section, we assume that the domain Ω is the entire space \mathbb{R}^n . Here is the definition of traveling wave solutions.

Definition 3.1. We say that $N_m(x)$ is a traveling wave solution of (1.2) in $e = (e_1, \dots, e_n) \in \mathbb{R}^n$ direction if there exist a function W and a constant c such that $N_m(x) = W(x \cdot e - cm)$.

We are now ready to provide our main result of this section.

Theorem 3.1. There exists a speeding speed c^* associated to (1.1)-(1.2) of the following form

$$(3.3) \quad c^*(e) := 2\sqrt{\langle Ae, e \rangle \sqrt{f'(0) + \ln(g'(0))}} + e \cdot a,$$

such that initial data which is nonzero on a bounded set eventually spreads at speed c^* in e -direction and $e = (e_1, \dots, e_n)$ is a unit vector in \mathbb{R}^n . Here, the symbol \langle, \rangle stands for the dot product.

In one dimension that is $n = 1$ for $g(N) = N$ and $A = d$, the formula (3.3) when $e = \pm 1$ is the standard spreading speed c_{\pm}^* for the Fisher's equation provided in (3.2).

Consider the speed of propagation $c^*(e)$ in e -direction as a function of the nonzero advection a when $A = d(\delta_{i,j})_{i,j=1}^n$. For the direction $e = -\frac{a}{|a|}$, that is a unit vector, from (3.3) we have

$$(3.4) \quad c^*\left(-\frac{a}{|a|}\right) = 2\sqrt{d}\sqrt{f'(0) + \ln(g'(0))} - |a|.$$

Note that $c^*\left(-\frac{a}{|a|}\right)$ vanishes exactly at $|a| = 2\sqrt{d[f'(0) + \ln(g'(0))]}$ for which the critical domain dimensions in Theorem 2.1 and Corollary 2.1 tend to infinity. The following figure together with Figure 1 clarify this relation.

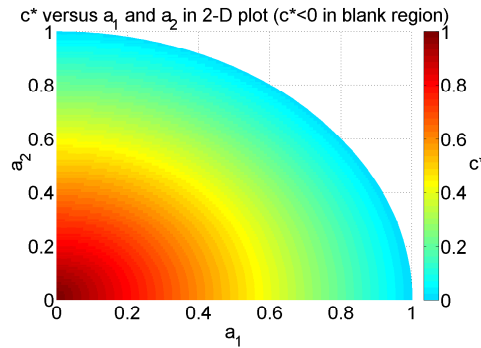


FIGURE 2. Spreading speed $c^*(e)$ when $A = dI$ in the direction $e = -\frac{a}{|a|}$ when $a = (a_1, a_2)$.

We end this section with an example in two dimensions. Set $e = (\cos \theta, \sin \theta)$, $A = a_{ij}^2 \delta_{ij}$ and $a = (a_1, a_2)$. Applying formula (3.3) we get

$$(3.5) \quad c^*(e) = 2\sqrt{a_{11}^2 \cos^2 \theta + a_{22}^2 \sin^2 \theta} \sqrt{f'(0) + \ln(g'(0))} + a_1 \cos \theta + a_2 \sin \theta,$$

where $0 \leq \theta < 2\pi$ and a_{11}, a_{22}, a_1, a_2 are constants. The latter formula clarifies the dependance of the spreading speed of propagation, for any angel θ , on anisotropic diffusion coefficients a_{11} and a_{22} and on advection coefficients a_1 and a_2 .

4. APPLICATIONS

In this section, we provide applications of main theorems given in the past sections.

4.1. Marine reserve. A marine reserve is a marine protected area against fishing and harvesting. Marine reserves could increase species diversity, biomass, and fishery production, etc. within reserve areas, Lockwood et al. (2002) in [29]. We use our model here to show the dependence of the critical domain size on the advection flow speed and the mortality rate. Consider the following model

$$(4.1) \quad \begin{cases} u_t = \operatorname{div}(d\nabla u - au) - \gamma u & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where γ is the natural mortality rate, and g is either the Beverton-Holt function $g(N_m) = \frac{(1+\lambda)N_m}{1+\lambda N_m}$ or the Ricker function $g(N_m) = N_m e^{r(1-N_m)}$. Since the assumption (1.14) holds, we suppose that $\ln(1+\lambda) > \gamma$ and $r > \gamma$. We now provide the critical dimension size regarding extinction versus persistence for various geometric shapes.

Case 1. Consider the domain $\Omega = [0, L] \times [0, L]$ in two dimensions. Then Theorem 2.1 implies that the critical dimension for the Beverton-Holt function is

$$(4.2) \quad L^*(a) = \frac{\pi\sqrt{2d}}{\sqrt{\ln(1+\lambda) - \gamma - \frac{|a|^2}{4d}}},$$

when $\ln(1+\lambda) > \gamma + \frac{|a|^2}{4d}$ and $L^*(a)$ can be arbitrarily large when $\gamma < \ln(1+\lambda) < \gamma + \frac{|a|^2}{4d}$. Similarly, for the Ricker function the critical dimension is

$$(4.3) \quad L^*(a) = \frac{\pi\sqrt{2d}}{\sqrt{r - \gamma - \frac{|a|^2}{4d}}},$$

when $r > \gamma + \frac{|a|^2}{4d}$ and $L^*(a)$ can be arbitrarily large when $\gamma < r < \gamma + \frac{|a|^2}{4d}$. In other words, when $L < L^*(a)$ the functional sequence $N_m(x)$ satisfies $\lim_{m \rightarrow \infty} N_m(x) = 0$ that refers to extinction and when $L > L^*(a)$ we have the persistence that is $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$ for the positive equilibrium $\bar{N}(x)$.

Case 2. Consider the domain $\Omega = B_R$ where B_R is a disk in two dimensions with radius R and a is a divergence free vector field. Theorem 2.2 implies that the critical value dimension for the Beverton-Holt function is

$$(4.4) \quad R^*(\gamma) = j_{0,1} \sqrt{\frac{d}{\ln(1+\lambda) - \gamma}},$$

and for the Ricker function the critical dimension is

$$(4.5) \quad R^*(\gamma) = j_{0,1} \sqrt{\frac{d}{r - \gamma}},$$

where $j_{0,1} \approx 2.408$ is the first positive root of the Bessel function J_0 . In other words, for subcritical radius that is when $R < R^*(\gamma)$ we have $\lim_{m \rightarrow \infty} N_m(x) = 0$ and for supercritical radius that is when $R > R^*(\gamma)$ we have $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$ for some positive equilibrium $\bar{N}(x)$.

Case 3. Consider a general domain Ω in two dimensions with smooth boundary and area $|\Omega|$. In addition, let a be a divergence free vector field that is $\text{div } a = 0$. We now apply Theorem 2.3 to find the following extreme harvesting parameter

$$(4.6) \quad \gamma_{ex} := \frac{dj_{0,1}^2}{|\Omega|} - \ln(1 + \lambda),$$

that implies for $\gamma < \gamma_{ex}$ extinction occurs for the Beverton-Holt function. Similarly for the Ricker function the extreme harvesting parameter h is given by

$$(4.7) \quad \gamma_{ex} := \frac{dj_{0,1}^2}{|\Omega|} - r.$$

Note that our main results regarding the critical domain size and the extreme volume size (Section 2) are valid in three dimensions as well. As an application of these results, one can consider the water volume of a marine reserve region for coral reef fish. Reserves are being applied popularly to conserve coral reef fish populations under threat, see [3, 32]. It is important to estimate the minimum reserve volume for the persistence of marine fish populations. Theorem 2.3 imply that ocean currents could not improve the persistence of a reserved marine species, under the assumption of hostile boundary conditions at the exterior of the reserve and under the assumption that the dynamics follow the given equations in the model.

4.2. Terrestrial reserve. A terrestrial reserve is a terrestrial protected area for conservation and economic purposes. Terrestrial reserves would conserve biodiversity and protect threatened and endangered species from hunting [14]. We use our model here to show the dependence of terrestrial species persistence on the diffusion rate. Consider

$$(4.8) \quad \begin{cases} u_t = d\Delta u - \gamma u & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where g is the Beverton-Holt function $g(N_m) = \frac{(1+\lambda)N_m}{1+\lambda N_m}$. Since the assumption (1.14) holds, we suppose that $\ln(1 + \lambda) > \gamma$.

Case 1. Consider the domain $\Omega = [0, L_1] \times [0, L_2]$ in two dimensions where L_1, L_2 are positive. Then a direct consequence of Theorem 2.1 is that when the diffusion is greater than the following critical diffusion

$$(4.9) \quad d^* := \frac{1}{\pi^2} [\ln(1 + \lambda) - \gamma] \frac{L_1^2 L_2^2}{L_1^2 + L_2^2},$$

that is when $d > d^*$ we have $\lim_{m \rightarrow \infty} N_m(x) = 0$ that refers to extinction. In addition, when $d < d^*$ we have $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$ for some positive equilibrium $\bar{N}(x)$.

Case 2. We now consider a bounded domain Ω in two dimensions with a smooth boundary and area $|\Omega|$. Theorem 2.3 implies that when the diffusion is greater than the following extreme diffusion

$$(4.10) \quad d_{ex} := \frac{|\Omega|}{\pi j_{0,1}^2} [\ln(1 + \lambda) - \gamma],$$

that is when $d > d_{ex}$ then population must go extinct. Note that for the case of $\Omega = B_R$, Theorem 2.2 implies that the extreme diffusion given by (4.10) is the critical diffusion

$$(4.11) \quad d^* := \frac{R^2}{j_{0,1}^2} [\ln(1 + \lambda) - \gamma],$$

meaning that when $d > d^*$ then $\lim_{m \rightarrow \infty} N_m(x) = 0$ and for $d < d^*$ we have $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$ for some positive equilibrium $\bar{N}(x)$. In Case 1, we considered a rectangular domain that does not have smooth boundaries unlike the domain in Case 2. Comparing d^* and d_{ex} given by (4.9) and (4.10) one sees that $d^* < d_{ex}$ when $\Omega = [0, L_1] \times [0, L_2]$ and $L_1 = L_2$, since $\pi j_{0,1}^2 \approx 18.21$ and $2\pi^2 = 19.73$.

4.3. Insect pest outbreaks. Insect pest outbreak is a historic problem in agriculture and can have long-lasting effects. It may be necessary to control insect pests in order to maximize crop production [41]. We apply our model here to study the dependence of insect pest extirpation on the removal rate. Consider

$$(4.12) \quad \begin{cases} u_t = d\Delta u + r(1-u)u & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where $g(N_m) = (1-s)N_m$ and $0 < s < 1$ is the fraction of pests surviving periodic control. The assumption (1.14) implies that $e^r(1-s) > 1$.

Case 1. Consider the rectangular domain $\Omega = [0, L_1] \times [0, L_2]$ in two dimensions for positive L_1, L_2 . We now apply Theorem 2.1 to conclude that the critical value for the parameter s regarding extinction versus persistence is

$$(4.13) \quad s^* := 1 - e^{d\pi^2 \left[\frac{L_1^2 + L_2^2}{L_1^2 L_2^2} \right] - r}.$$

More precisely, for $s > s^*$ we have $\lim_{m \rightarrow \infty} N_m(x) = 0$ and for $s < s^*$ we have $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$ for the positive equilibrium $\bar{N}(x)$.

Case 2. Consider a slightly more general bounded domain Ω in two dimensions with a smooth boundary and area $|\Omega|$. Here we introduce an extreme value for the parameter s as

$$(4.14) \quad s_{ex} := 1 - e^{\frac{d\pi^2 j_{0,1}^2}{|\Omega|} - r},$$

meaning that when s is larger than s_{ex} the population must go extinct.

4.4. Population subject to climate change. Climate change, especially global warming, has greatly changed the distribution and habitats of biological species. Uncovering the potential impact of climate change on biota is an important task for modelers [37]. We investigate the dependence of the critical domain size and the spreading speed on the climate shifting speed.

We consider a rectangular domain that is $\Omega = [0, L_1] \times [0, L_2]$ moving in the positive x -axis direction at speed c . Outside this domain conditions are hostile to population growth, while inside the domain there is random media, mortality and periodic reproduction. Using the approach of [37] this problem is transformed to a related problem on a stationary domain. Consider the model:

$$(4.15) \quad \begin{cases} u_t = d\Delta u + a \cdot \nabla u - \gamma u & \text{for } (x, t) \in \Omega \times (0, 1], \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times (0, 1], \\ u(x, 0) = g(N_m(x)) & \text{for } x \in \Omega, \\ N_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega, \end{cases}$$

where g is the Beverton-Holt function that is $g(N_m) = \frac{(1+\lambda)N_m}{1+\lambda N_m}$ and the vector field a is non zero in x -axis direction that is $a = (-c, 0)$. Similar to previous examples the assumption (1.14) implies that $\ln(1+\lambda) > \gamma$. Theorem 2.1 implies that for

$$(4.16) \quad \frac{1}{L_1^2} + \frac{1}{L_2^2} < \frac{1}{d\pi^2} \left[\ln(1+\lambda) - \gamma - \frac{c^2}{4d} \right],$$

when $\ln(1+\lambda) > \gamma + \frac{c^2}{4d}$ we have $\lim_{m \rightarrow \infty} N_m(x) = \bar{N}(x)$ for some positive equilibrium $\bar{N}(x)$ which refers to persistence of population. In other words, (4.16) yields the parameter c must be bounded by

$$(4.17) \quad c^2 < 4d[\ln(1+\lambda) - \gamma] - (2d\pi)^2 \left[\frac{L_1^2 + L_2^2}{L_1^2 L_2^2} \right] < 4d[\ln(1+\lambda) - \gamma].$$

Let us mention that Theorem 3.1 implies that the speed of propagation for the model (4.15) on an infinite domain $\Omega = \mathbb{R}$ in the x -axis direction is

$$(4.18) \quad c^* = 2\sqrt{d[\ln(1+\lambda) - \gamma]} - c.$$

Note that when c satisfies (4.17) then the speed of propagation in (4.18) is positive. This implies that persistence and ability to propagate should be closely connected. This is the case from a biological perspective as well. For example, if a population cannot propagate upstream but is washed downstream, it will not persist. We refer interested readers to Speirs and Gurney [40] and Pachepsky et al. [35] for similar arguments regarding Fisher's equation with advection. Note also that the speed of propagation vanishes in (4.18) exactly at the values that make the right-hand side of (4.16) zero when the critical domain dimensions, L_1 and L_2 , approach infinity. One can compare this relation to the one given in (1.4) and (1.5) for the classical Fisher's equation.

5. DISCUSSION

We examined impulsive reaction-diffusion equation models for species with distinct reproductive and dispersal stages on domains $\Omega \subset \mathbb{R}^n$ when $n \geq 1$ with diverse geometrical structures. Unlike standard partial differential equation models, study of impulsive reaction-diffusion models requires a simultaneous analysis of the differential equation and the recurrence relation. This fundamental fact rules out certain standard mathematical analysis theories for analyzing solutions of these type models, but it opens up various ways to apply the model. These models can be considered as a description for a continuously growing and dispersing population with pulse harvesting and a population with individuals immobile during the winter. As a domain Ω for the model, we considered bounded sets in \mathbb{R}^n , including convex and non convex domains with smooth or non smooth boundaries, and also the entire space \mathbb{R}^n . Since the geometry of the domain has tremendous impacts on the solutions of the model, we consider various type domain to study the qualitative properties of the solutions. We refer interested readers to [9, 10, 13] and references therein regarding *how habitat edges change species interactions*.

On bounded rectangular and circular domains, we provided critical domain sizes regarding persistence versus extinction of populations in any space dimension $n \geq 1$. In order to find the critical domain sizes we used the fact that the first eigenpairs of the Laplacian operator for such domains can be computed explicitly. Note that for a general bounded domain in \mathbb{R}^n , with smooth boundaries, the spectrum of the Laplacian operator is not known explicitly. However, various estimates are known for the eigenpairs. As a matter of fact, study of the eigenpairs of differential operators is one of the oldest problems in the field of mathematical analysis and partial differential equations, see Faber [15], Krahn [24], Pólya [36] and references therein.

We applied several mathematical analysis methods like Schwarz symmetrization rearrangement arguments, the classical Rayleigh-Faber-Krahn inequality and lower bounds for the spectrum of uniformly elliptic operators with Dirichlet boundary conditions given by Li-Yau [28] to compute a novel quantity called extreme volume size. Whenever $|\Omega|$ falls below the extreme volume size the species must driven extinct, regardless of the geometry of the domain. In other words, the extreme volume size provides a lower bound (a necessary condition) for the persistence of population. In the context of biological sciences this can provide a partial answer to questions about *how much habitat is enough?*, see Fahrig [14] and references therein. We believe that this opens up new directions of research in both mathematics and sciences. Throughout this paper we assumed that the diffusion matrix and the advection vector field contain constant components. Study of the influence of non constant advection and non constant diffusion on persistence and extinction properties can be considered along the work of Hamel and Nadirashvili [18] and Hamel, Nadirashvili and Russ [19].

On the entire space \mathbb{R}^n , we provided an explicit formula for the spreading speed of propagation in any direction $e \in \mathbb{R}^n$ in terms of the same set of model parameters used for computing critical domain sizes and extreme volume sizes. The spreading speed formula was first computed by Kolmogoroff, Petrowsky, and Piscounoff (KPP) and Fisher in 1937 for the semilinear parabolic equation $u_t - \Delta u = f(u)$ when $(x, t) \in \mathbb{R}^n \times \mathbb{R}^+$. They proved that under certain assumptions on f , now called KPP nonlinearities, there is a threshold value $c^* = 2\sqrt{f'(0)}$ such that there is no front for $c < c^*$ and for all $c \geq c^*$ there is a unique front up to translations and dilations in terms of space and time. Study of the minimal speed of propagation and the asymptotic spreading speed has attracted the attention of many mathematicians and scientists for the past few decades, see [1, 2, 15, 17, 43, 44]. Many authors have driven formulae for the spreading speed of propagation for parabolic equations with a non constant diffusion matrix and a non constant advection vector field on cylinders, periodic domains and general domains, see Gärtner-Freidlin [17], Mallordy-Roquejoffre [30], Heinze-Papanicolaou-Stevens [20], Berestycki-Hamel-Nadirashvili [4, 5] and references therein. In these articles, authors used variational principles, more precisely min-max theories, to express the spreading speed

formulae. One can apply the ideas and mathematical techniques used in these references to develop a theory of propagation for the impulsive reaction-diffusion equation models with a non constant diffusion matrix and a non constant advection vector with hostile and flux boundary conditions.

We now compute the asymptotic speed of propagation for a large drift and for a large diffusion. Here M stands for a large constant.

- Large drift. If a is replaced by Ma , then the spreading speed in e -direction converges to

$$\lim_{M \rightarrow \infty} \frac{c_M^*(e)}{M} = e \cdot a.$$

- Large diffusion. If A is replaced by M^2A , then the minimal spreading speed in e -direction converges to

$$\lim_{M \rightarrow \infty} \frac{c_M^*(e)}{M} = 2\sqrt{\langle Ae, e \rangle} \sqrt{f'(0) + \ln(g'(0))}.$$

Note that the asymptotic spreading speed (both existence and the exact quantity) for parabolic KPP equations with non constant diffusion and advection on general and periodic domains has been studied extensively in the literature, see Berestycki-Hamel-Nadirashvili [4, 5], Bhattacharya-Gupta-Walker [7], Zlatos [45], Smalley-Kirsch [11] and references therein. This naturally brings up the question that what are the asymptotic spreading speed of propagation for impulsive reaction-diffusion models with non constant diffusion and advection. Note that to study impulsive reaction-diffusion models one needs to do simultaneous analysis of differential equations and recurrence relations. Therefore, some standard mathematical techniques applied in the literature does not work directly for our current model.

Our results show a strong connection between persistence criteria and propagation speeds just like in the case of Fisher-KPP equation, for more information see [15, 25, 33–35]. In particular, the spreading speed $c^*(e)$ in direction $e = -\frac{a}{|a|}$ at which the critical domain size is infinite is the same as the spreading speed for which the population switches from spreading upstream to retreating. Note that when $n = 1$ our results recovers the results provided by Lewis and Li [26] and when $g(N) = N$ and $A = d(\delta_{i,j})_{i,j=1}^n$ our results on both bounded and unbounded domains coincide with the ones for the standard Fisher-KPP equation. We also presented applications of our main results in two and three space dimensions to certain biological reaction-diffusion models regarding marine reserve, terrestrial reserve, insect pest outbreaks and population subject to climate change.

6. PROOFS

In this section, we provide mathematical proofs for our main results.

6.1. Proofs of Theorem 2.1 and Theorem 2.2. We start with the proof of Theorem 2.1. Proof of Theorem 2.2 is very similar. For both of the proofs, the following technical lemma plays a fundamental role. We shall omit the proof of the lemma since it is standard in this context.

Lemma 6.1. *Suppose that ϕ_1, λ_1 are the first eigenvalue and the first eigenfunction of (2.17). Then*

$$(6.1) \quad \lambda_1(dI, a, [0, L_1] \times \cdots \times [0, L_n]) = \frac{|a|^2}{4d} + d\pi^2 \left(\frac{1}{L_1^2} + \cdots + \frac{1}{L_n^2} \right),$$

$$(6.2) \quad \lambda_1(dI, 0, B_R) = j_{n/2-1,1}^2 R^{-2}d,$$

where $j_{m,1}$ is the first positive zero of the Bessel function J_m .

Proof of Theorem 2.1. Suppose that the recurrence relation $\bar{N}_m(x)$ is a solution of the following linearized problem

$$(6.3) \quad \begin{cases} u_t + a \cdot \nabla u = \operatorname{div}(A \nabla u) + f'(0)u & \text{for } (x, t) \in \Omega \times \mathbb{R}^+, \\ u(x, t) = 0 & \text{for } (x, t) \in \partial\Omega \times \mathbb{R}^+, \\ u(x, 0) = g'(0)\bar{N}_m(x) & \text{for } x \in \Omega, \\ \bar{N}_{m+1}(x) := u(x, 1) & \text{for } x \in \Omega. \end{cases}$$

Let

$$(6.4) \quad u(x, t) = cg'(0)e^{\lambda t}\phi(x),$$

be a solution for the above linear problem (6.3) for some function ϕ and constant c . It is straightforward to show that ϕ satisfies

$$(6.5) \quad -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi = (f'(0) - \lambda)\phi \quad \text{in } \Omega.$$

Note that the initial condition is $u(x, 0) = g'(0)\bar{N}_m(x) = cg'(0)\phi(x)$. This implies that

$$(6.6) \quad \bar{N}_{m+1}(x) = u(x, 1) = cg'(0)e^\lambda\phi(x) = g'(0)e^\lambda\bar{N}_m(x).$$

In the light of (6.5), we consider the following Dirichlet eigenvalue problem

$$(6.7) \quad \begin{cases} -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi &= \lambda\phi \quad \text{in } \Omega, \\ \phi &= 0 \quad \text{on } \partial\Omega, \\ \phi &> 0 \quad \text{in } \Omega, \end{cases}$$

and let the pair $(\phi_1, \lambda_1(A, a, \Omega))$ be the first eigenpair of this problem. Setting $\lambda := f'(0) - \lambda_1(A, a, \Omega)$ in (6.4) we get

$$(6.8) \quad u(x, t) = cg'(0)e^{(f'(0) - \lambda_1(A, a, \Omega))t}\phi_1(x).$$

This implies that

$$(6.9) \quad \bar{N}_{m+1}(x) = c \left(g'(0)e^{f'(0) - \lambda_1(A, a, \Omega)} \right)^m \phi_1(x).$$

Therefore, we get

$$(6.10) \quad \lim_{m \rightarrow \infty} \bar{N}_m(x) = 0,$$

when $g'(0)e^{f'(0) - \lambda_1(A, a, \Omega)} < 1$, that is when

$$(6.11) \quad \lambda_1(A, a, \Omega) > \ln(e^{f'(0)}g'(0)).$$

Suppose that $u(x, 0) = N_0(x)$ is an initial value for the original nonlinear problem (1.1). One can choose a sufficiently large c such that $N_0(x) \leq \bar{N}_0(x)$. Applying standard comparison theorems, together with the fact that g is linear, and induction arguments we obtain $N_m(x) \leq \bar{N}_m(x)$ for all $m \geq 0$. This implies that

$$(6.12) \quad \lim_{m \rightarrow \infty} N_m(x) = 0,$$

when (6.11) holds. We now analyze inequality (6.11) that involves the first eigenvalue of (6.7). Applying Lemma 6.1 to (6.7) when $A = d(\delta_{i,j})_{i,j=1}^n$, $\Omega = [0, L_1] \times \cdots \times [0, L_n]$ we obtain

$$(6.13) \quad \lambda_1(dI, a, \Omega) = \frac{|a|^2}{4d} + d\pi^2 \left(\sum_{i=1}^n L_i^{-2} \right).$$

Equating this and (6.11) we end up with

$$(6.14) \quad \sum_{i=1}^n L_i^{-2} > \frac{1}{4d^2\pi^2} \left[4d[\ln(e^{f'(0)}g'(0))] - |a|^2 \right].$$

This proves the first part of the theorem. To show the second part we suppose that g is upper sublinear and we analyze the eigenvalue problem (6.7). Suppose that $g'(0)e^{f'(0) - \lambda_1(A, a, \Omega)} > 1$ that is when the inequality (6.11) is reversed, namely,

$$(6.15) \quad \lambda_1(A, a, \Omega) < \ln(g'(0)) + f'(0).$$

Let $\underline{\lambda} > \lambda_1$ and \underline{g} such that $\underline{g}e^{f'(0) - \underline{\lambda}} > 1$. Since g is upper sublinear, there exist a \tilde{M} such that $g(N) \geq g'(0)N - h(N)$ for $0 < N < \tilde{M}$. The fact that h is differentiable and $h(0) = h'(0) = 0$ implies that there exists a positive constant δ such that for $N < \delta$ the fraction $\frac{h(N)}{N}$ can be sufficiently small, let's say

$$(6.16) \quad \frac{h(N)}{N} < \min\{g'(0) - \underline{g}, \underline{\lambda} - \lambda_1\}.$$

Now define

$$(6.17) \quad \underline{u}(x, t) = \underline{g}e^{(f'(0) - \underline{\lambda})t}\phi_1(x).$$

Note that $g(\underline{u}(x, t)) \geq g'(0)\underline{u}(x, t) - h(\underline{u}(x, t))$. For sufficiently small ϵ and $t \in (0, 1]$, we get

$$(6.18) \quad \frac{g(\underline{u}(x, t))}{\underline{u}(x, t)} \geq \underline{g} + (g'(0) - \underline{g}) - \frac{h(\underline{u}(x, t))}{\underline{u}(x, t)} \geq \underline{g},$$

where we have used the fact that $\frac{h(\underline{u}(x, t))}{\underline{u}(x, t)} < g'(0) - \underline{g}$ when $t \in (0, 1]$. This implies that

$$(6.19) \quad g(\underline{u}(x, t)) \geq \underline{g} \underline{u}(x, t).$$

We now show that \underline{u} is a subsolution for the partial differential equation given in (1.1) when $t \in (0, 1]$ that is

$$(6.20) \quad u_t = \operatorname{div}(A \nabla u) + a \cdot \nabla u + f(u).$$

Note that f is an upper sublinear function. This implies that

$$(6.21) \quad \begin{aligned} & \underline{u}_t - \operatorname{div}(A \nabla \underline{u}) - a \cdot \nabla \underline{u} - f(\underline{u}) \\ & \leq \epsilon \underline{g} e^{(f'(0) - \underline{\lambda})t} [(f'(0) - \underline{\lambda})\phi_1 - \operatorname{div}(A \nabla \phi_1) + a \cdot \nabla \phi_1 - f'(0)\phi_1] + h(\underline{u}) \\ & = \epsilon \underline{g} e^{(f'(0) - \underline{\lambda})t} [-\operatorname{div}(A \nabla \phi_1) + a \cdot \nabla \phi_1 - \lambda_1 \phi_1] \\ & \quad + \epsilon \underline{g} e^{(f'(0) - \underline{\lambda})t} [\lambda_1 - \underline{\lambda}] \phi_1 + h(\underline{u}). \end{aligned}$$

Note that λ_1 is the first eigenvalue of (6.7) that yields

$$(6.22) \quad -\operatorname{div}(A \nabla \phi_1) + a \cdot \nabla \phi_1 - \lambda_1 \phi_1 = 0.$$

Applying this in (6.23) we get

$$(6.23) \quad \begin{aligned} & \underline{u}_t - \operatorname{div}(A \nabla \underline{u}) - a \cdot \nabla \underline{u} - f(\underline{u}) \\ & \leq \epsilon \underline{g} e^{(f'(0) - \underline{\lambda})t} [\lambda_1 - \underline{\lambda}] \phi_1 + h(\underline{u}) \\ & = \underline{u} \left[\lambda_1 - \underline{\lambda} + \frac{h(\underline{u})}{\underline{u}} \right]. \end{aligned}$$

We now apply (6.16) to conclude that

$$(6.24) \quad \underline{u}_t - \operatorname{div}(A \nabla \underline{u}) - a \cdot \nabla \underline{u} - f(\underline{u}) \leq 0.$$

This proves our claim. Suppose that $N_m(x)$ is a solution of (1.1) then

$$(6.25) \quad N_{m+1}(x) = Q[g(N_m)](x),$$

where the operator Q maps $u(x, 0)$ to $u(x, 1)$. To be more precise, let $u(x, t)$ solve

$$(6.26) \quad \begin{cases} u_t = \operatorname{div}(A \nabla u - au) + f(u) & \text{for } (x, t) \in \Omega \times (0, 1] \\ u(x, 0) = u_0(x) & \text{for } x \in \Omega \end{cases}$$

then $u(x, 1) = Q[u_0](x)$. It is straightforward to see that Q is a monotone operator due to comparison principles. Now, let $M_0(x) = \epsilon \phi_1(x)$ and

$$(6.27) \quad M_{m+1}(x) = Q[g(M_m)](x).$$

From (6.24) we know that \underline{u} is a subsolution. Therefore,

$$(6.28) \quad Q[g(M_0)](x) \geq Q[\underline{g} M_0](x) \geq \underline{u}(x, 1) \geq M_0(x).$$

An induction argument implies that

$$(6.29) \quad M_{m+1}(x) \geq M_m(x) \quad \text{for } m \geq 0.$$

For sufficiently large ϵ , $M_0(x) = \epsilon \phi_1(x) \leq N^*$ where N^* is a positive equilibrium for (1.12). Therefore,

$$(6.30) \quad M_m(x) \leq M_{m+1}(x) \leq N^*.$$

The sequence of function $M_m(x)$ is bounded increasing that must be convergent to $N(x)$. Note also that for sufficiently small ϵ we get $M_0(x) \leq N_1(x)$ and from comparison principles we have $M_{m+1}(x) \leq N_m(x)$. This and (6.30) imply that $\liminf_{m \rightarrow \infty} N_m(x) \geq \liminf_{m \rightarrow \infty} M_m(x) = N(x)$. This completes the proof. \square

Proof of Corollary 2.1. Assuming that $L_i = L > 0$ for any $1 \leq i \leq n$, from (6.14) we get the following

$$(6.31) \quad nL^{-2} > \frac{1}{4d^2\pi^2} (4d[\ln(g'(0)) + f'(0)] - |a|^2).$$

This completes the proof. \square

Proof of Theorem 2.2. Suppose that the recurrence relation $\bar{N}_m(x)$ is a solution of the linearized problem (6.3) when $\operatorname{div} a = 0$ and $A = d(a_{i,j})_{i,j=1}^m$. Assume that the following function $u(x, t)$ is a solution for the linear problem (6.3),

$$(6.32) \quad u(x, t) = cg'(0)e^{\lambda t}\phi(x),$$

for some constant c and where ϕ satisfies

$$(6.33) \quad -d\Delta\phi + a \cdot \nabla\phi = (f'(0) - \lambda)\phi \quad \text{in } B_R.$$

Suppose that λ_1 is the first eigenvalue of the following eigenvalue problem with Dirichlet boundary conditions

$$(6.34) \quad \begin{cases} -d\Delta\phi + a \cdot \nabla\phi = \lambda(dI, a, B_R)\phi & \text{in } B_R \\ \phi = 0 & \text{on } \partial B_R \\ \phi > 0 & \text{in } B_R \end{cases}$$

Under similar arguments as in the proof of Theorem 2.1, whenever

$$(6.35) \quad \lambda_1(dI, a, B_R) > \ln(e^{f'(0)}g'(0)),$$

we conclude the following decay

$$(6.36) \quad \lim_{m \rightarrow \infty} N_m(x) = \lim_{m \rightarrow \infty} \bar{N}_m(x) = 0 \quad \text{in } B_R,$$

and otherwise we get

$$(6.37) \quad \lim_{m \rightarrow \infty} N_m(x) \geq \lim_{m \rightarrow \infty} \bar{N}_m(x) \geq N(x) \quad \text{in } B_R.$$

Therefore, we only need to discuss the magnitude of λ_1 . Lemma 6.1 implies that

$$(6.38) \quad \lambda_1(dI, 0, B_R) = d \left(\frac{|B_1|}{|B_R|} \right)^{2/n} j_{n/2-1,1}^2,$$

where $j_{n/2-1,1}$ is the first positive zero of the Bessel function $J_{n/2-1}$. This and the fact that a is a divergence free vector field implies that

$$(6.39) \quad \lambda_1(dI, a, B_R) \geq dR^{-2}j_{n/2-1,1}^2.$$

Combining (6.39) and (6.35) provides proofs for (6.36) and (6.37) when $R < R^*$ and $R > R^*$, respectively, where

$$(6.40) \quad R^* := \sqrt{\frac{d j_{n/2-1,1}^2}{\ln(g'(0)) + f'(0)}}.$$

This completes the proof. \square

6.2. Proofs of Theorem 2.3 and Theorem 2.4. This part is dedicated to proofs of theorems regarding the extreme volume size for both a general domain $\Omega \subset \mathbb{R}^n$ with a smooth boundary, Theorem 2.3, and also for a n -hyperrectangle domain $\Omega = [0, L_1] \times \cdots \times [0, L_n]$ with non smooth boundaries, Theorem 2.4.

Proof of Theorem 2.3. With the same reasoning as in the proof of Theorem 2.1, the limit tends to zero that is

$$(6.41) \quad \lim_{m \rightarrow \infty} N_m(x) = \lim_{m \rightarrow \infty} \bar{N}_m(x) = 0 \quad \text{in } \Omega,$$

when

$$(6.42) \quad \lambda_1(A, a, \Omega) > \ln(e^{f'(0)}g'(0)).$$

Here $\lambda_1(A, a, \Omega)$ stands for the first eigenvalue of

$$(6.43) \quad \begin{cases} -\operatorname{div}(A\nabla\phi) + a \cdot \nabla\phi &= \lambda_1(A, a, \Omega)\phi & \text{in } \Omega, \\ \phi &= 0 & \text{on } \partial\Omega, \\ \phi &> 0 & \text{in } \Omega. \end{cases}$$

From the fact that the vector field a is divergence free (in the sense of distributions), we have $\lambda_1(A, a, \Omega) \geq \lambda_1(A, 0, \Omega)$. This can be seen by multiplying (6.43) with ϕ and integrating by parts over Ω and using the fact that $\operatorname{div} a = 0$. We now apply the generalized Rayleigh-Faber-Krahn inequality (2.18) that is

$$(6.44) \quad \lambda_1(A, a, \Omega) \geq \lambda_1(dI, 0, \Omega^*),$$

where Ω^* is the ball $B_R \subset \mathbb{R}^n$ for the radius $R = \left(\frac{|\Omega|}{|B_1|}\right)^{1/n}$ where $|B_1|$ is the volume of the unit ball that is $|B_1| = \frac{\pi^{\frac{n}{2}}}{\Gamma(1+\frac{n}{2})}$. Note that Lemma 6.1 implies that

$$(6.45) \quad \lambda_1(dI, 0, \Omega^*) = j_{n/2-1,1}^2 R^{-2} d.$$

Combining (6.42), (6.44) and (6.45) shows that whenever

$$(6.46) \quad j_{n/2-1,1}^2 R^{-2} d > f'(0) + \ln(g'(0)),$$

the decay estimate (6.41) holds. Note that the radius R in (6.46) is $\left(\frac{|\Omega|}{|B_1|}\right)^{1/n}$. This implies that for any domain with the volume $|\Omega|$ that is less than

$$(6.47) \quad |\Omega| < |B_1| \left(\frac{d j_{n/2-1,1}^2}{f'(0) + \ln(g'(0))} \right)^{\frac{n}{2}},$$

the population must go extinct. This completes the proof. \square

We now provide a proof for Theorem 2.4 that is in regards to n -hyperrectangle domain $\Omega = [0, L_1] \times \cdots [0, L_n]$ with non smooth boundaries.

Proof of Theorem 2.4. The idea of proof is very similar to the ones provided in proofs of Theorem 2.3 and Theorem 2.1. The decay of the $N_m(x)$ to zero as m goes to infinity refers to inequality (6.14) that is

$$(6.48) \quad \frac{1}{L_1^2} + \cdots + \frac{1}{L_n^2} > \frac{1}{d\pi^2} \left[f'(0) + \ln(g'(0)) - \frac{|a|^2}{4d} \right].$$

Note that when the right-hand side of the above inequality is nonpositive then this is valid for any L_i for $1 \leq i \leq n$. So, we assume that $f'(0) + \ln(g'(0)) - \frac{|a|^2}{4d} > 0$.

On the other hand, the following inequality of arithmetic and geometric means hold

$$(6.49) \quad \frac{1}{L_1^2} + \cdots + \frac{1}{L_n^2} \geq n \sqrt[n]{\frac{1}{L_1^2} \cdots \frac{1}{L_n^2}} = n \left(\frac{1}{L_1 \cdots L_n} \right)^{\frac{2}{n}} = n |\Omega|^{-\frac{2}{n}},$$

where the equality holds if and only if $L_1 = \cdots = L_n$. Combining (6.48) and (6.49) yields that when

$$(6.50) \quad |\Omega| < \left(\frac{nd\pi^2}{f'(0) + \ln(g'(0)) - \frac{|a|^2}{4d}} \right)^{n/2},$$

the population must go extinct. This completes the proof. \square

6.3. The spectrum of the Laplacian operator. To find the extreme volume size V_{ex} in Theorem 2.3 we applied the Schwarz symmetrization argument and the classical Rayleigh-Faber-Krahn inequality and its generalizations. In this part we discuss that one can avoid applying rearrangement type arguments to obtain inequalities for eigenvalues of the Laplacian operator with Dirichlet boundary conditions for an arbitrary domain Ω . However, the extreme volume size V_{ex} that we deduce with this argument is slightly smaller than the one given in (2.20). Suppose that

$$(6.51) \quad \begin{cases} -\Delta\phi &= \lambda\phi & \text{in } \Omega, \\ \phi &= 0 & \text{on } \partial\Omega, \\ \phi &> 0 & \text{in } \Omega. \end{cases}$$

The discreteness of the spectrum of the Laplacian operator allows one to order the eigenvalues $0 < \lambda_1 \leq \lambda_2 \leq \dots \leq \lambda_k \leq \dots$ monotonically. Proving lower bounds for λ_k has been a celebrated problem in the field of partial differential equations. We now mention key results in the field and then we apply the lower bounds to our models. In 1912, H. Weyl showed that the spectrum of (6.51) has the following asymptotic behaviour as $k \rightarrow \infty$,

$$(6.52) \quad \lambda_k \sim (2\pi)^2 |B_1|^{-\frac{2}{n}} \left(\frac{k}{|\Omega|} \right)^{\frac{2}{n}}.$$

In 1960, Pólya in [36] proved that for certain geometric shapes that is “plane-covering domain” $\Omega \subset \mathbb{R}^n$ the following holds for all $k \geq 1$,

$$(6.53) \quad \lambda_k \geq (2\pi)^2 |B_1|^{-\frac{2}{n}} \left(\frac{k}{|\Omega|} \right)^{\frac{2}{n}}.$$

Then he conjectured that the above inequality should hold for general domains in \mathbb{R}^n . His original proof and his conjecture were provided for $n = 2$. Even though this conjecture is still an open problem there are many interesting results in this regard. The inequality

$$(6.54) \quad \lambda_k \geq C_n (2\pi)^2 |B_1|^{-\frac{2}{n}} \left(\frac{k}{|\Omega|} \right)^{\frac{2}{n}},$$

with a positive constant $C_n < \frac{n}{n+2}$ was given for arbitrary domains in [?] and references therein. Li and Yau [28] improved upon this result, proving that the following lower bound holds for all $k \geq 1$,

$$(6.55) \quad \lambda_k \geq \frac{n}{n+2} (2\pi)^2 |B_1|^{-\frac{2}{n}} \left(\frac{k}{|\Omega|} \right)^{\frac{2}{n}}.$$

We now apply the lower bound (6.55) to get the following extreme volume size. Note that this V_{ex} is independent from Bessel functions.

Theorem 6.1. *Let $A = d(\delta_{i,j})_{i,j=1}^m$ for a positive constant d , functions f, g be sublinear satisfying (1.14) and the vector field a be divergence free. Suppose that $\Omega \subset \mathbb{R}^n$ is an open bounded domain with smooth boundary and $|\Omega| < V_{ex}$ where*

$$(6.56) \quad V_{ex} = \Gamma\left(1 + \frac{n}{2}\right) \left[\frac{4dn\pi}{(n+2)[f'(0) + \ln(g'(0))]} \right]^{\frac{n}{2}}.$$

Then $\lim_{m \rightarrow \infty} N_m(x) = 0$ for any $x \in \Omega$.

Corollary 6.1. *In two dimensions $n = 2$, the extreme volume size provided in (6.56) is*

$$(6.57) \quad V_{ex} = \frac{2d\pi}{f'(0) + \ln(g'(0))}.$$

Moreover, in three dimensions $n = 3$, the extreme volume size (6.56) simplifies to

$$(6.58) \quad V_{ex} = \frac{18\sqrt{3}\pi^2}{5\sqrt{5}} \left(\frac{d}{f'(0) + \ln(g'(0))} \right)^{\frac{3}{2}},$$

where we have used the fact that $\Gamma(1 + \frac{n}{2}) = \Gamma(\frac{5}{2}) = \frac{3\sqrt{\pi}}{4}$.

Note that V_{ex} given in (6.57) and (6.58) are slightly smaller than the ones given by (2.21) and (2.22) in Corollary 2.2 and Corollary 2.3, respectively.

Proof of Theorem 6.1. Note that we have the following lower bound on the first eigenvalue as an immediate consequence of (6.55), that is

$$(6.59) \quad \lambda_1(dI, 0, \Omega) \geq d \frac{n}{n+2} (2\pi)^2 (|B_1| |\Omega|)^{-\frac{2}{n}}.$$

Following ideas provided in the proof of Theorem 2.3 one can complete the proof. \square

We finish this section with a sketch of proof for the spreading speed provided in Theorem 3.1.

6.4. Proof of the spreading speed formula. First note that for a symmetric positive definite matrix $A = (a_{i,j})_{i,j=1}^n$ with constant components, the following integration formulae hold;

$$(6.60) \quad \int_{\mathbb{R}^n} e^{iz \cdot \eta - \langle A\eta, \eta \rangle} d\eta = \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} e^{-\frac{1}{4} \langle A^{-1} z, z \rangle},$$

and

$$(6.61) \quad \int_{\mathbb{R}^n} e^{z \cdot \eta - \langle A^{-1} \eta, \eta \rangle} d\eta = \pi^{\frac{n}{2}} \sqrt{\det A} e^{\frac{1}{4} \langle Az, z \rangle},$$

for any $z \in \mathbb{R}^n$ where $\langle A\eta, \eta \rangle$ stands for $\eta^T A \eta$ for any $\eta \in \mathbb{R}^n$. The ideas and method that we apply here are strongly motivated by the ones derived by Weinberger in [43, 44] and applied in [25–27, 42]. Suppose that $L[N]$ is the linearization of operator $Q[N]$ about zero. Define $M_0(x) := N_0(x)$ then $M_{m+1}(x) = L[M_m(x)]$ where

$$(6.62) \quad \begin{cases} u_t + a \cdot \nabla u = \operatorname{div}(A \nabla u) + f'(0)u & \text{for } (x, t) \in \mathbb{R}^n \times \mathbb{R}^+, \\ u(x, 0) = g'(0)M_m(x) & \text{for } x \in \mathbb{R}^n, \\ M_{m+1}(x) := u(x, 1) & \text{for } x \in \mathbb{R}^n. \end{cases}$$

Note that $\operatorname{div}(A \nabla u) = \sum_{i,j} a_{ij} u_{x_i x_j}$. Let the notation \mathcal{F} stand for the Fourier transform that is

$$(6.63) \quad \mathcal{F}(u)(\zeta, t) = (2\pi)^{-\frac{n}{2}} \int_{\mathbb{R}^n} e^{-ix \cdot \zeta} u(x, t) dx.$$

From properties of Fourier transform we have

$$(6.64) \quad \mathcal{F}(u_{x_i x_j})(\zeta, t) = -\zeta_i \zeta_j \mathcal{F}(u)(\zeta, t) \quad \text{and} \quad \mathcal{F}(a \cdot \nabla u)(\zeta, t) = ia \cdot \zeta \mathcal{F}(u)(\zeta, t).$$

Applying the Fourier transform to (6.62) we get

$$(6.65) \quad \partial_t \mathcal{F}(u)(\zeta, t) + ia \cdot \zeta \mathcal{F}(u)(\zeta, t) = - \sum_{i,j} a_{ij} \zeta_i \zeta_j \mathcal{F}(u)(\zeta, t) + f'(0) \mathcal{F}(u)(\zeta, t).$$

This is a first order differential equation with an initial value $\mathcal{F}(u)(\zeta, 0) = g'(0) \mathcal{F}(M_m)(\zeta)$. Applying the method of characteristics we get

$$(6.66) \quad \mathcal{F}(u)(\zeta, t) = g'(0) \mathcal{F}(M_m)(\zeta) e^{tf'(0) - t(ia \cdot \zeta + \sum_{i,j} a_{ij} \zeta_i \zeta_j)}.$$

For some $k(x, t)$, define

$$(6.67) \quad \mathcal{F}(k)(\zeta, t) := (2\pi)^{-\frac{n}{2}} e^{tf'(0) - t(ia \cdot \zeta + \sum_{i,j} a_{ij} \zeta_i \zeta_j)}.$$

Therefore, $\mathcal{F}(u)(\zeta, t) = (2\pi)^{\frac{n}{2}} g'(0) \mathcal{F}(M_m)(\zeta) \mathcal{F}(k)(\zeta, t)$. From the properties of the Fourier transform we have

$$(6.68) \quad u(x, t) = g'(0) \int_{\mathbb{R}^n} k(x - y, t) M_m(y) dy,$$

where

$$(6.69) \quad k(x, t) = e^{tf'(0)} (2\pi)^{-n} \int_{\mathbb{R}^n} e^{ix \cdot \zeta} e^{-t(ia \cdot \zeta + \sum_{i,j} a_{ij} \zeta_i \zeta_j)} d\zeta,$$

$$(6.70) \quad = e^{tf'(0)} (2\pi)^{-n} \int_{\mathbb{R}^n} e^{i(x-ta) \cdot \zeta} e^{-t \sum_{i,j} a_{ij} \zeta_i \zeta_j} d\zeta.$$

Now set $\eta = \zeta\sqrt{t}$. Then

$$(6.71) \quad k(x, t) = e^{tf'(0)}(2\pi)^{-n}t^{-\frac{n}{2}} \int_{\mathbb{R}^n} e^{i\left(\frac{x-ta}{\sqrt{t}}\right) \cdot \eta - \langle A\eta, \eta \rangle} d\eta.$$

Applying (6.60) with $z = \frac{x-ta}{\sqrt{t}}$ for any $x \in \mathbb{R}^n$ and $t \in \mathbb{R}^+$ we get the following explicit formula for k

$$(6.72) \quad k(x, t) = e^{tf'(0)}(2\pi)^{-n}t^{-\frac{n}{2}} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} e^{-\frac{1}{4}\langle A^{-1}\left(\frac{x-ta}{\sqrt{t}}\right), \left(\frac{x-ta}{\sqrt{t}}\right) \rangle}.$$

We now substitute the above formula for k in (6.68) to obtain

$$(6.73) \quad u(x, t) = g'(0)e^{tf'(0)}(2\pi)^{-n}t^{-\frac{n}{2}} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} \int_{\mathbb{R}^n} e^{-\frac{1}{4}\langle A^{-1}\left(\frac{x-y-ta}{\sqrt{t}}\right), \left(\frac{x-y-ta}{\sqrt{t}}\right) \rangle} M_m(y) dy.$$

Note that $M_{m+1}(x) = u(x, 1)$. Therefore, setting $t = 1$ in the above implies

$$(6.74) \quad \begin{aligned} M_{m+1}(x) &= g'(0)e^{f'(0)}(2\pi)^{-n} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} \int_{\mathbb{R}^n} e^{-\frac{1}{4}\langle A^{-1}(x-y-a), (x-y-a) \rangle} M_m(y) dy \\ &= L[M_m(x)]. \end{aligned}$$

Note that the operator L is defined on the set of all continuous functions as

$$(6.75) \quad \begin{aligned} L(v)(x) &:= g'(0)e^{f'(0)}(2\pi)^{-n} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} \int_{\mathbb{R}^n} e^{-\frac{1}{4}\langle A^{-1}(y-a), (y-a) \rangle} v(x-y) dy \\ &= \int_{\mathbb{R}^n} v(x-y) m(y, dy), \end{aligned}$$

where the measure m is defined as

$$(6.76) \quad m(y, dy) := g'(0)e^{f'(0)}(2\pi)^{-n} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} e^{-\frac{1}{4}\langle A^{-1}(y-a), (y-a) \rangle}.$$

Note that $m(y, dy)$ is a bounded nonnegative measure, since A is a positive definite matrix. The operator $L[v]$ behaves continuously with respect to changes in v . Here we emphasize on a few properties of the operator L . The operator L commutes with any translation, meaning

$$(6.77) \quad L[T_y[v]](x) = T_y[L[v]](x),$$

when T is the shift operator $T_y[v](x) = v(x-y)$. In addition, the comparison principle holds for the operator L meaning that for $v_1 \leq v_2$ we have $L[v_1](x) \leq L[v_2](x)$, due to properties of the integral operator. Let us recall that the integral operator is continuous with respect to its integrand. This elementary fact implies that when $v_n \rightarrow v$ as $n \rightarrow \infty$ uniformly then $L[v_n](x) \rightarrow L[v](x)$. On the other hand, it is straightforward calculation to show that

$$(6.78) \quad \int_{\mathbb{R}^n} m(x, dx) = g'(0)e^{f'(0)}.$$

Combining this and condition (1.14) that is $g'(0)e^{f'(0)} > 1$, we get $\int_{\mathbb{R}^n} m(x, dx) > 1$. Note that the latter is an assumption of Theorem 6.4 in [43]. We assumed earlier that $\frac{g(N)}{N}$ is a nonincreasing function of N in \mathbb{R}^+ that is

$$(6.79) \quad \frac{g(M)}{M} \geq \frac{g(N)}{N} \quad \text{for } N \geq M.$$

Now set $M = \rho N \leq N$ for $0 \leq \rho \leq 1$ and apply the above inequality to get

$$(6.80) \quad g(\rho N) \geq \rho g(N).$$

This implies that for all $0 \leq \rho \leq 1$ we have

$$(6.81) \quad Q[\rho u] \geq \rho Q[u],$$

where u is a solution of (1.1) and Q is given by (1.2). In short, operators L and Q and the measure m satisfy all of the assumptions of Theorem 6.3 and Theorem 6.4 provided by Weinberger in [43] regarding the spreading speed. Therefore,

$$(6.82) \quad c^*(e) = \inf_{\mu > 0} \frac{1}{\mu} \ln \int_{\mathbb{R}^n} e^{\mu x \cdot e} m(x, dx),$$

when $m(x, dx)$ satisfies (6.76). We now compute the integral in the right-hand side of (6.82)

$$\begin{aligned} \int_{\mathbb{R}^n} e^{\mu x \cdot e} m(x, dx) &= g'(0) e^{f'(0)} (2\pi)^{-n} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} \int_{\mathbb{R}^n} e^{\mu x \cdot e - \frac{1}{4} \langle A^{-1}(x-a), (x-a) \rangle} dx \\ &= g'(0) e^{f'(0)} (2\pi)^{-n} (2)^n \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} \int_{\mathbb{R}^n} e^{\mu e \cdot (2\eta + a) - \langle A^{-1}\eta, \eta \rangle} d\eta \\ (6.83) \quad &= g'(0) e^{f'(0)} (\pi)^{-n} e^{\mu e \cdot a} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} \int_{\mathbb{R}^n} e^{\eta \cdot (2\mu e) - \langle A^{-1}\eta, \eta \rangle} d\eta. \end{aligned}$$

Applying formula (6.61) for $z = 2\mu e$ we obtain

$$\begin{aligned} \int_{\mathbb{R}^n} e^{\mu x \cdot e} m(x, dx) &= g'(0) e^{f'(0)} (\pi)^{-n} e^{\mu e \cdot a} \frac{\pi^{\frac{n}{2}}}{\sqrt{\det A}} \pi^{\frac{n}{2}} \sqrt{\det A} e^{\frac{1}{4} \langle A(2\mu e), (2\mu e) \rangle} \\ (6.84) \quad &= g'(0) e^{f'(0)} e^{\mu e \cdot a + \mu^2 \langle Ae, e \rangle}. \end{aligned}$$

Substituting (6.84) in (6.82) and computing the infimum we finally get

$$(6.85) \quad c^*(e) = 2\sqrt{\langle Ae, e \rangle} \sqrt{f'(0) + \ln(g'(0))} + e \cdot a,$$

when $g'(0)e^{f'(0)} > 1$. This is the formula for the speed of propagation that is used in (4.18). Note that when $g(N) = N$, $A = d(\delta_{i,j})_{i,j=1}^n$ and $a = 0$ we get $c^* = 2\sqrt{df'(0)}$ that is the speed of propagation for the Fisher's model. We refer interested readers to [1, 2, 15, 25, 33, 34, 44] for more information regarding propagation phenomenon for reaction-diffusion models.

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